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Throscidae (Coleoptera) relationships, with descriptions of new fossil genera and species

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Abstract

Two new Throscidae genera from Baltic amber are described: *Tyrannosthroscus* n. gen. (type species *Tyrannothroscus rex* n. sp.) and *Pseudothroscus* n. gen. (type species *Pseudothroscus balticus* n. sp.). Four species are described from Baltic amber: *Tyrannothroscus rex* n. sp., *Pseudothroscus balticus* n. sp., *Potergus superbus* n. sp. and *Trixagus parvulus* n. sp. *Pactopus burmensis* n. sp. is described from Burmese amber. A phylogenetic analysis of the known throscid genera is performed. *Aulonothroscus* Horn and *Trixagus* Kugelann are shown to be sister-groups, the sister-group of this clade is the genus *Pactopus* Horn and the sister group of these three genera is the genus *Potergus* Bonvouloir. The oldest previously known throscids were species belonging to the genera *Rhomboaspis* Kirejtshuk & Kovalev and *Potergosoma* Kirejtshuk & Kovalev, both from Lebanese Amber, 125…135 Mya. The present analysis shows that the extinct Baltic amber genera *Jaira* Muona and *Pseudothroscus* belong to clades at least as old as the Lebanese fossils. The Burmese amber fossil *Pactopus burmensis*, 99 Mya, is considerably older than any of the previously known species belonging to the four extant genera *Pactopus*, *Potergus*, *Aulonothroscus* or *Trixagus*. At least three throscid lineages are now known to have gone extinct. Both the *Pactopus* and *Potergus* lineages are more than 99 milion years old, whereas the *Aulonothroscus* and *Trixagus* lineages extend at least to the Baltic amber, 50 million years ago. The presence of *Jaira* in Baltic amber shows that that lineage persisted at least 80 million years before going to extinction.

Key words: Amber fossil, phylogeny, ghost taxa, Elateroidea, relationships

Introduction

Throscidae is a small, apomorphic beetle family belonging to the superfamily Elateroidea (Muona *et al.* 2010). Eight genera are included in it presently. Crowson (1955) included Lissominae and Thylacosterninae in Throscidae as well, but analyses based on both morphological and sequence data place them in Elateridae (Lawrence 1988; Muona 1995; Lawrence *et al.* 2007; Vahtera *et al.* 2009; Kundrata *et al.* 2014). These studies agree on two points: Throscidae and Eucnemidae are closely related, and they form a more basal grouping than the Lycidae-Lampyridae-Cantharidae-Elateridae lineage. The monophyly of the throscids as defined today appears well established, but the relationships of the genera included have never been studied analytically. Examination of tropical material indicates that the generic limits of the two extant speciose genera, *Trixagus* Kugelann and *Aulonothroscus* Horn, are not clear. The pre-1960 fossil throscid descriptions were reviewed by Cobos (1963) and Muona (1993). Three fossil throscid genera have been described since then (Muona 1993; Kovalev *et al.* 2013) and the discovery of further unusual fossil forms suggests that an analysis of the within-family relationships is needed.

What then are the synapomorphies defining a throscid and what are the diagnostic characters needed to recognize one? Two of the throscid features Kovalev *et al.* (2013) list appear to be plesiomorphies: free labrum and pocket-type metacoxal plates are the states found in most basal Elateriformia. The enlarged apical antennomeres is a feature found in several lineages within polyphagan beetles, e.g. many basal eucnemids, and is probably a feature useful for identification only. The unusual antennal grooves Kovalev *et al.* (2013) mention are a unique feature, and might be regarded as a putative throscid synapomorphy. Finally, the wide, flat prosternal process may well be a throscid synapomorphy as well.

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Characters. Both specimens and information from literature were used for coding the characters. The special structures of the throscid head and eyes are illustrated in detail in Coffin (1993). The general morphology and genital anatomy of *Throscus* and *Aulonothroscus* are illustrated in Burakowski (1975, 1991), and those of *Potergus* in Cobos (1961). Characters not explained in these references are illustrated in this article.

Three characters are commonly used to identify the extant genera *Trixagus* and *Aulanothroscus*: form of the eyes and the presence or absence of frontal keels and metathoracic tarsal grooves. These occur in different combinations and six species were included in the analysis to cover this variation.

All the fossil species studied are samples embedded in Amber. MicroCT-scanning was not available for studying the material. This was less of a handicap for the Baltic Amber samples, but the older Burmese and Lebanese samples would provide more information with this method. New features could be detected from the Lebanese specimens with use of variable lighting, however.

0. Eyes: entire or slightly emarginate = 0; halfway emarginate = 1; nearly entirely divided = 2; with keeled emargination = 3.
1. Eyes: without supraocular groove = 0; with supraocular groove = 1.
2. Head below antennal insertion: simple = 0; with subantennal pit = 1.
3. Head: without subantennal groove = 0; with subantennal groove = 1.
4. Antennomere a2: narrower than a3…a5 = 0; wider than a3…a5 = 1.
5. Apical antennomeres 9…11: at most slightly symmetrically enlarged = 0; forming distinct, symmetrical club = 1; forming asymmetrical flattened club = 2.
6. Antennal insertions: exposed = 0 (Fig. 1); located in circular fossae = 1 (Fig. 5).
7. Frontoclypeal region at midline: steeply sloping = 0; steeply sloping, with transverse carinae = 1.
8. Head at midline: simple = 0; with sharp carina = 1.
9. Head: without longitudinal ridges = 0; with ridges on both sides = 1.
10. Propleurocoxal articular area: well-developed = 0; absent = 1.
11. Prosternum: without paired carinae = 0; with carinae half-way thorugh = 1; with nearly complete carinae = 2; with complete carinae = 3; with faintly indicated carinae in middle = 4.
12. Prosternal process in lateral view: curved from base to apex = 0; straight basally; abruptly elevated apically = 1. 13. Lateral pronotal carinae: complete = 0; vanishing anteriorly = 1.
14. Prothoracic antennal grooves: absent = 0; running by the notosternal suture and extending posteriolaterad along the hind margins of the hypomera = 1.
15. Antennal grooves posteriorly: partly separated from proleg impressions by septum = 1; separated from proleg impressions by septum = 2.
16. Pro- and mesoleg impressions: extend posteriorly as well-defined metathoracic tarsal grooves = 0; extend posteriorly as vestigial grooves = 1; not present = 2. Yensen (1975) seems to be the only author correctly describing this feature. Usually *Trixagus* is claimed •not to haveŽ such tarsal grooves, although vestigial ones are present (Fig. 2).
17. Mesocoxal cavity: not present = 0; deep = 1.
18. Metacoxal plates: Much wider medially than laterally = 0; parallel = 1; throscid-type, medially extending posteriorly = 2 (Fig. 6).
19. Abdomen: without tarsal grooves = 0; with tarsal impressions = 1; with tarsal gooves = 2.
20. Protibiae: with two spurs = 0; without spurs = 1.
21. Meso- and metatibiae: simple, apically unmodified = 0 (Fig. 5); simple, apically abruptly widening = 1; with lateral shap carinae = 2; with lateral sharp carinae and apically enlarged = 3 (Fig 12).
22. Protrochanter: less than twice as long as wide = 0; more than twice as long as wide = 1.
23. Elytra: with punctate striae = 0; with strong and deep faintly punctate striae = 1; with well-defined sharp gutter-like neatly punctate striae = 2; with stongly and coarsely punctate striae = 3.
24. Metathoracic discrimen: well developed = 0; present, but faint = 1; absent = 2.
25. Tergite VIII: with spiracles = 0; without spiracles = 1. .
26. Median lobe: longer than parameres = 0; shorter than parameres = 1. .
27. Radial cell: closed = 0; open = 1. .

28. Number of free veins in the medial field: five = 0; four = 1; three = 2.
29. Male sternite VIII: caudally rounded = 0; caudally emarginate = 1.
30. Meso-metaventral junction: even = 0; bifid, projecting cranially as a large letter "V" = 1 Fig. 18).
31. Meso- and metatarsomere 4: simple = 0; lobed = 1.
32. Protibiae: slender, without tarsal groove = 0; flattened, with tarsal grooves = 1.
33. Prosternum anteriorly: with chin piece = 0; chin piece with ventrally directed lip = 1 (Fig. 7).

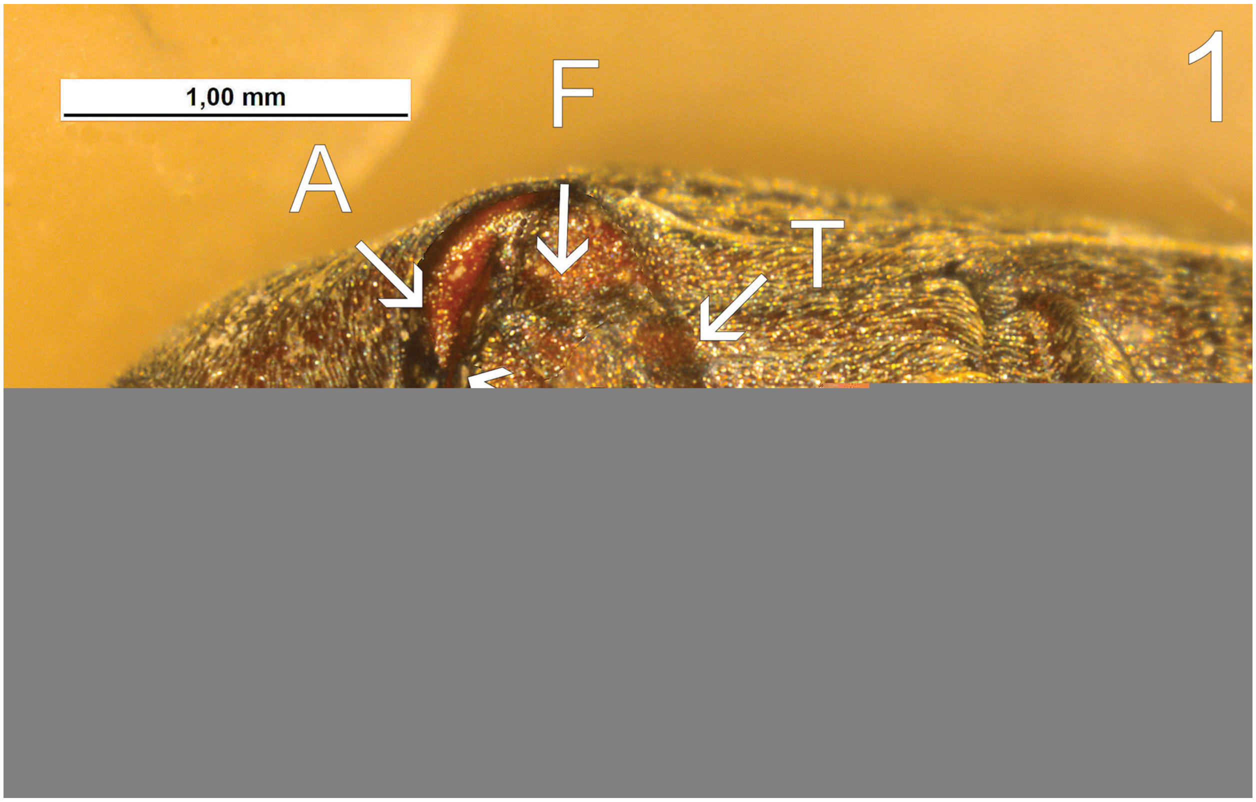

FIGURE 1. *Pactopus horni* LeConte. Head and thorax, ventrolateral view. A = antennal groove; F = depression for mesofemur; M = mesothoracic tarsal groove; mc = mesocoxa; pc = procoxa; S = septum; T = depression for mesotibia.

Character distribution.

TABLE 1. Character matrix.

Phyllocerus	000100000010000-310000000000000000
Brachypsectra	000000000010000--01010100-00000000
Pactopus_horni	0001110000021111012212021001100010
Pactopus_burmensis	0001110000021111012212031?????0010
Trixagus carinifrons	2111120001031112112113022101200110
Trixagus stanleyi	2111120000031112112113022101200110
Trixagus dermestoides	1111120001031112112113022101200110
Aulonothroscus species	3101120001031112012113022111200110
Aulonothroscus brevicollis	0101120001031112012113022111200110
Aulonothroscus laticollis	0101120000031112012113022111200110
Cryptophthalma	2??112000103111201211302211???0110
Pseudothroscus	00?1111000?310112120?2?32?????0000
Potergosoma	???1111010?310112120?2?22??????000
Rhomboaspis	00?1111000?310120122?2?12?????1001
Tyrannothroscus	01?1111100?31012012212010?????0101
Potergus_freyi	0001111010041012012212001001110010
Potergus_superbus	0001111010041012012212031?????0010
Jaira	00?1111010?1101?2110?1?30?????0100

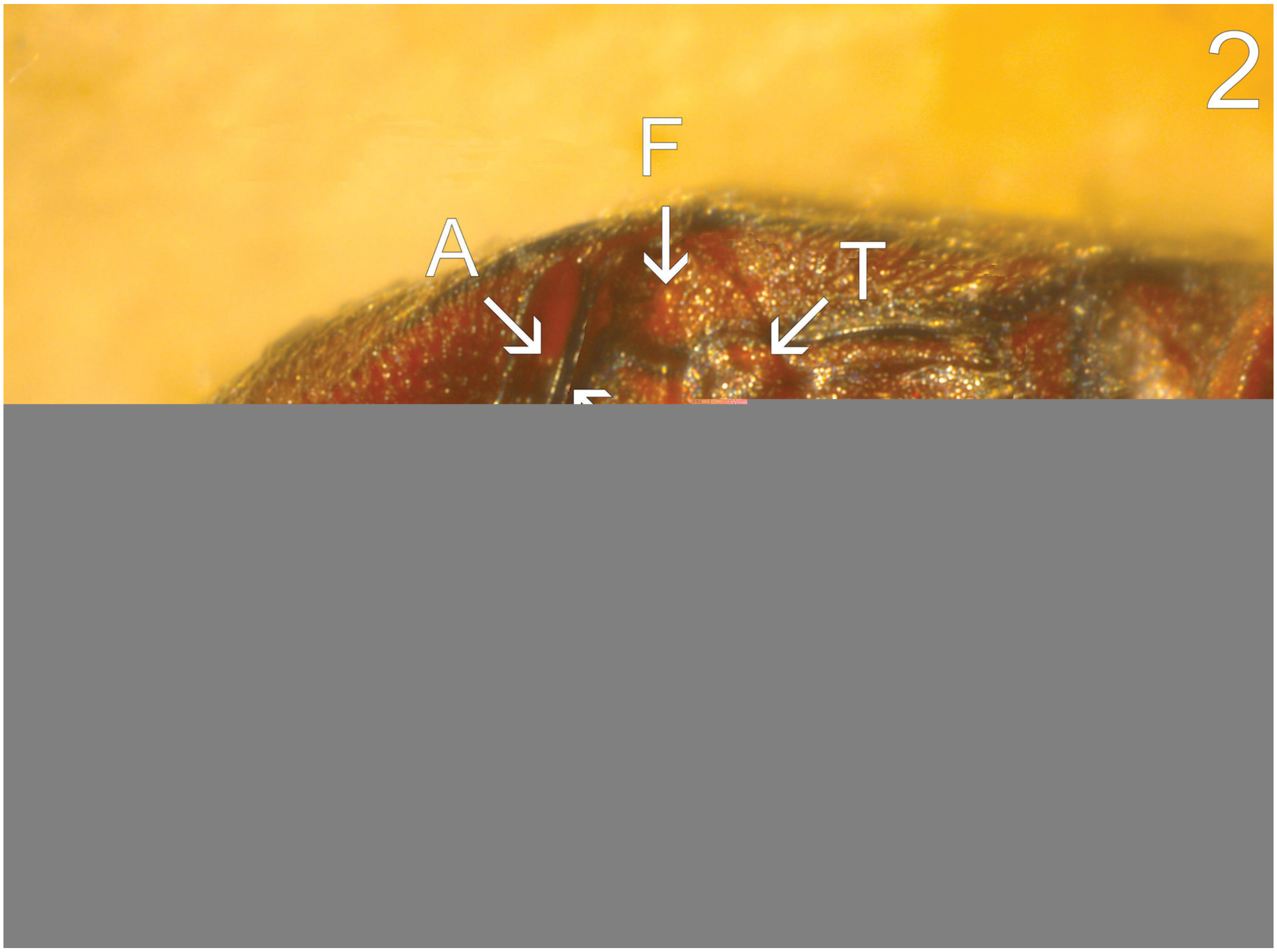

FIGURE 2. *Trixagus carinifrons* (Bonvouloir). Head and thorax, ventrolateral view. A = antennal groove; F = depression for mesofemur; M = mesothoracic tarsal groove; mc = mesocoxa; pc = procoxa; S = septum; T = depression for mesotibia.

Taxa included in the analysis. *Phyllocerus* was included as the out-group in the analysis and *Brachyspectra* as a possible sister-group of Throscidae.

Aulonothroscus Horn, 1890
(= *Throscites* Yablokoff-Khnzorian, 1962)
World-wide today, but most described species are tropical. Fossils are known from Eocene Baltic Amber (50 Mya, Muona 1993).
A. brevicollis (Bonvouloir). Finland, Sa: Savonlinna (JMC); •GermanyŽ (JMC); Turkey, Bolghar Dagh (FMNH). Both sexes.
A. laticollis (Rybinski). Finland (FMNH). Both sexes.
A. sp. Australia, NSW: Wiangaree (JMC). Both sexes.

Brachypsectra LeConte
B. sp. The characters were taken from Lawrence *et al.* (2007) and Costa *et al.* (2010).

Cryptophthalma Cobos, 1982
C. alvarengai Cobos. Brazil. Scored from the original description (Cobos 1982).

Jaira Muona, 1993
J. bella Muona. Baltic Amber. Coded from Muona (1993) and unpublished photographs.

Pactopus LeConte, 1868
Western North America. Fossils are known from Miocene Colorado (Wickham 1916), Eocene London Clay (Britton 1960), Eocene Baltic Amber (50 Mya, Muona 1993) and Cretaceous Burmese Amber (99 Mya, this article). Several undescribed species are known from Baltic Amber.
P. horni LeConte. USA, Mendocino Co., (JMC). Both sexes.
P. burmensis **n. sp.** Burmese Amber (99 Mya, JMC).

Phyllocerus Lepeletier & Serville, 1825
South and Central eastern Africa, Madagascar and Palaearctic.
P. flavipennis Lepeletier & Serville. •ItalyŽ (JMC). Both sexes.

Potergosoma Kovalev & Kirejtshuk, 2013 in Kovalev, Kirejtshuk and Azar 2013
Cretaceous Lebanese Amber (130 Mya, Kovalev *et al.*, 2013)
P. gratiosa Kovalev, Kirejtshuk. The unique holotype was studied (MHNP).

Potergus Bonvouloir 1859
Two described species are known from Indonesia and Australia, several undescribed ones exist in the Old World tropics. Fossils are known from Eocene Baltic Amber (50 Mya, Muona 1993, this article).
P. freyi Cobos. New Guinea, Gazelle Peninsula (BBMH). Both sexes.
P. superbus **n.sp**. Eocene Baltic Amber (50 Mya, JMC).

Pseudothroscus **n. gen.**
Eocene Baltic Amber (50 Mya, this article).
P. balticus **n. sp.** The unique holotype was studied (JMC).

Rhomboaspis Kovalev & Kirejtshuk 2013 in Kovalev, Kirejtshuk & Azar, 2013
Cretaceous Lebanese Amber (130 Mya, Kovalev *et al.*, 2013)
R. laticollis Kovalev, Kirejtshuk. The unique holotype was studied (MHNP).

Trixagus Kugelann, 1794
(= *Palaeothroscus* Yablokoff-Khnzorian 1962)
World-wide, but most described species are Holarctic. Fossils are known from Eocene Baltic amber, but they are scarce (50 Mya, Muona 1993, this article).
T. dermestoides (Linnaeus). Finland, Ab: Raasepori, Karjaa (JMC), many, both sexes.
T. carinifrons (Bonvouloir). Finland, Ab: Raasepori, Karjaa (JMC), many, both sexes.
T. stanleyi (Cobos). •KenyaŽ (JMC). Both sexes.

Tyrannothroscus **n. gen.**
Eocene Baltic Amber (50 Mya, this article).
T. rex **n. sp.** The unique holotype was studied (JMC).

Collection abbreviations:

JMC = Author•s collection, presently in the Finnish Museum of Natural History.
MHNP = Museum d•Histoire Naturelle, Paris

Analysis and results. The matrix was built with Winclada (Nixon 2002) and analyzed with PARANONA, a multithread version of NoNa (Goloboff 1994). All characters were treated as unordered and the optimality criterion was parsimony. *Phyllocerus* was used as the outgroup and *Brachyspectra* was included in the ingroup as a possible sister-group to all throscids. Traditional search using two threads, 200 replicates of random addition sequences and both TBR adn SBR (•mult*200; max*;Ž) resulted in four trees of length 60 steps. After collapsing nodes not supported under all optimizations and disregarding suboptimal trees, three trees were obtained (Figs. 19…21). The exactly same result could be obtained by using a 200 replicate ratchet search as implemented in WinClada (Nixon, 2002).

The results are identical except for the apical clade including the *Aulonothroscus* and *Trixagus* species. In tree 1 (Fig. 19) the apical clade is supported by seven synapomorphies: eyes with supraocular groove (0:1), antennal club flattened (5:2), abdomen with tarsal impressions (19:1), meso- and metatibiae carinate, apically abruptly enlarged (21:3), tergite eight without spiracles (25:1), metathoracic wings with three free median field veins (28.2) and meso- and metatarsomere four lobed (31:1). The monophyly of the genus *Aulonothroscus* is supported by one synapomorphy, median lobe being shorter than parameres (26:1), whereas three characters support the monophyly of the genus *Trixagus*: nearly completely divided eyes (0:2), head with subantennal pit (2:1) and vestigial pro- and mesoleg grooves (16:1).

The *Aulanothroscus* + *Trixagus* group is monophyletic in trees 2 and 3 as well (Figs. 20, 21), but in these trees only *Trixagus* is monophyletic. The apical group is supported by seven synapomorphies as it was in tree 1, but one character is not included and another one added. Character 25 is no longer included as a synapomorpy. It could not be checked from three of the seven species and could not be optimized unambiguously on the topologies shown on trees 2 and 3. The new synapomorphy for the combined clade in topologies 2 and 3 is •median lobe shorter than parameresŽ (26:1).

FIGURE 3. *Potergus freyi* Cobos. Head and thorax, ventrolateral view. A = antennal groove; F = depression for mesofemur; M = mesothoracic tarsal groove; mc = mesocoxa; pc = procoxa; S = septum; T = depression for mesotibia; X = secondary septum.

The fundamental difference between the topologies is whether the short male median lobe type is a synapomorphy for the *Aulonothroscus*-*Trixagus* species, having then reversed to the plesiomorphic elateroid state in *Trixagus*, OR a synapomorphy of the genus *Aulonothroscus*. As both solutions are equally correct, i.e. the trees are of equal length, it seems reasonably to opt for tree one and regard *Aulonothroscus* and *Trixagus* as monophyletic sister-groups. *Cryptophthalma* appears to be an autapomorphic *Aulanothroscus*, but this question cannot be solved here.

The analysis cannot be regarded as a strong test for Throscidae monophyly as neither Cerophytidae nor Eucnemidae were included. The putative throscid apomorphies found were a2 wider than a3 to a5 (character 4:1), apical antennomeres forming a distinct club (character 5:1), antennal insertions located in circular fossae (character 6:1), prosternal process basally staright, apically abruptly elevated (character 12:1), prothoracic antennal grooves running along the notosternal suture and extending posterolaterally along the hind margins of the hypomera (character 14:1) and elytra with coarsely punctate striae (character 23:3). Characters 4:1 and 14:1 are useful for identification as well, the others less so as they appear in different combinations in other Elateriformia. The antennal club, often considered an unusual feature in this series, actually characterizes several basal lineages of the Eucnemidae and may be a plesiomorphy when a wider sampling is employed.

Discussion. Cobos (1961) was the first one to discuss the relationships between the genera *Aulonothroscus*, *Trixagus*, *Pactopus* LeConte and *Potergus* Bonvouloir, but he did not attempt to formally analyze the data. He came to the conclusion that *Potergus* should be placed in a tribe of its own, Potergini, and the three remaining genera belonged to Throscini *s. str.* This is in agreement with the present results and the fossils added in the analysis strengthen this hypothesis. Kovalev *et al.* (2013) discussed the same question, but they did not try to analyze the material either. They noted that the new genera they described could not be placed in Cobos• system, but the characters observed suggested relationship with *Potergus* rather than the Throscini. The features they referred to as indicating relationship with *Potergus* are plesiomorphies in the present analysis and in that sense the